XXIV. *Observations upon the Anatomy and Physiology of* Salpa *and* Pyrosoma.

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1. The *Salpæ*, those strange gelatinous animals, through masses of which the voyager in the great ocean sometimes sails day after day, have been the subject of great controversy since the time of the publication of the celebrated work of Chamisso, 'De Animalibus quibusdam è classe Vermium Linnæana.'

In this work were set forth, for the first time, the singular phenomena presented by the reproductive processes of these animals,—phenomena so strange, and so utterly unlike anything then known to occur in the whole province of zoology, that Chamisso's admirably clear and truthful account was received with almost as much distrust as if he had announced the existence of a veritable Peter Schlemihl.

In later days an opposite fate has fallen upon the statements in question. They have been made the keystone of a revived* theory, and the phenomena presented by the *Salpæ* have been cited as "glaring instances" of a law governing the vast majority of the lower invertebrata—the law of the "Alternation of Generations."

2. There appeared then to be two main points to be kept in view in examining the *Salpæ*:—1st. Are the statements made by Chamisso correct? and 2ndly, if they be correct, how far is the "alternation theory" a just and sufficient generalization of the phenomena?

3. These questions, however, could not be entered upon without a thorough preliminary study of the structure of the *Salpæ*, the opportunities for which are granted but to few.

Such opportunities were afforded to the writer of the present paper at Cape York, in November 1849: for a time the sea was absolutely crowded with *Salpæ*, in all states of growth, and of a size very convenient for examination. At subsequent periods the writer had occasion repeatedly to verify the results at which he had arrived, and to find strong analogical confirmation in the structure of *Pyrosoma* and other allied genera†.

* Not new, see (70.).

† Those who are acquainted with the nature of the service on which H.M.S. 'Rattlesnake' was engaged, will readily comprehend that the author's investigations were almost *necessarily* original, and independent of anything going on in Europe.

It is the more necessary to state this, as it will be seen, in the historical part of this paper, that M. Krohn,

4. It is proposed in the following pages to consider—

I. The structure of the species of *Salpa* examined.

II. The structure of *Pyrosoma*.

III. The homology of structure of *Salpa* and *Pyrosoma*, and of these with the ordinary Ascidians.

IV. The history of our knowledge of the *Salpæ*.

I. *The Structure of* Salpa.

5. Before entering upon this question, there is a point of some importance to be determined, as to the upper and lower surfaces, the anterior and posterior extremities of the *Salpæ*. Observation will not decide this apparently simple matter, for as the writer has frequently seen, they swim indifferently with either end forward and with either side uppermost; and the determinations of authors are most contradictory.

Throughout the present paper, that side on which the heart is placed will be considered as the dorsal side; that on which the ganglion and auditory vesicle are placed, as the ventral side. That extremity to which the mouth is turned will again be considered as the anterior extremity, the opposite as the posterior. Such a view of the case appears to be more harmonious with the determinations of corresponding parts in other animals than any other. In all the invertebrata the mouth end is always considered as the anterior, the heart side as the dorsal side.

6. The two so-called species of *Salpa* examined were the *S. democratica* of Forskahl, *spinosa* of Otto, and the *S. mucronata* of Forskahl, *pyramidalis* of Quoy and Gaimard. They are described by Sars as *S. spinosa* and *S. mucronata*, or rather as *S. spinosa, proles solitaria*, and *S. spinosa, proles gregaria*. This however begs the question, as to the truth of Chamisso's theory, and I shall therefore prefer to name the two forms I observed simply *Salpa* A and *Salpa* B.

At Cape York, and only there, these two forms were always obtained together. They were of about the same size, but so totally distinct in appearance, that, had they belonged to any other genus, they would have been justly regarded as separate species.

7. *Salpa* A (Plate XV. fig. 1).—The body is gelatinous, transparent and colourless, except the nucleus (*i*), which has a deep reddish-brown tint. It has a general square prismatic shape, and is abruptly truncated and somewhat convex at each extremity. The posterior extremity is provided with eight hornlike processes, which project backwards. Two of these are short and hook-like, placed one before the other in the median line at the posterior part of the superior surface. On the upper part of the

in the Ann. des Sciences for 1846, has completely anticipated the chief results arrived at, a fact of which the author was totally unaware until his arrival in England in the end of 1850.

Still, as M. Krohn gives merely his conclusions without details or figures, his promised memoir not having appeared (so far as the writer of the present paper is aware), it is hoped that this anticipation will, by showing that perfectly independent observers arrive at the same result, rather tend to increase than to diminish any weight that may be attached to the present researches.

lateral surfaces there is, on each side, a short process. From about midway between the upper and lower edges of this surface, a long, conical process curves upwards and backwards; these processes are distinguished from the others by containing a cæcal process of the system of sinuses in their base (*y*).

Close to the lower edge of the lateral surfaces there is another short process like the uppermost one.

The respiratory apertures are wide and provided with valvular lips. The posterior (*b*) is narrower, and has the valvular lip more marked.

The ganglion (*d*) is less than one-fourth of the length of the body distant from the anterior respiratory aperture.

The otolithes are four in number, hemispherical, and with a dark, blackish brown coloured spot on their external surface, Plate XVI. fig. 5.

The endostyle (*c*) is nearly half the length of the body (reaches as far as the sixth muscular band, counting from before backwards).

The outer surface of the integument is everywhere covered with minute asperities, like little prickles.

The muscular bands (*k*) are seven in number, and, with the exception of the anterior and posterior, completely encircle the body of the animal. This form was always free and solitary*.

8. *Salpa* B, Plate XV. fig. 2, on the other hand, is thus characterized. The body is subovoid, smaller at the posterior extremity than at the anterior (*a*); the former ends in a point, the latter in a small square facet.

The sides are flattened into several irregular facets, and the upper and lower edges are sometimes somewhat carinated. The apertures are similar in general structure to those of the form A, and the anterior and posterior extremities project considerably beyond them.

The ganglion (*d*) is placed at about one-fourth of the length of the body from the anterior extremity. The otolithes resembled those of A.

The endostyle (*c*) is not nearly equal in length to half the body; it does not extend so far back as to the third muscular band.

The outer surface of the integument is smooth.

The muscular bands (*k*) are five in number, and none of them encircle the body of the animal, the dorsal extremities being always separated by a considerable interval. This form, when young, was sometimes found in chains; the adults were always separate.

These forms, it will be observed, are widely different, and the difference is as great between the youngest forms of each as between the adults, so that they are not derived from one another by any species of metamorphosis, properly so called.

Whatever be their external differences, however, their internal organization is so similar that the same description applies to both.

* The statements of Meyen (*op. cit.*) to the contrary are certainly erroneous.

9. The *Salpa*, then, may be considered as a hollow cylinder, consisting of two tunics, an external and an internal (α, β), the former (α) forming the mantle, the latter (β) the wall of the respiratory cavity. These tunics are continuous with one another at the respiratory apertures, but elsewhere they are separated by a more or less wide space.

In very young *Salpæ* this space is like the cavity of a serous sac, but in the older forms it becomes broken up into smaller channels by the adhesion of the inner and outer tunics to one another at various places, and so constitutes a system of sinuses; it may be conveniently called the "sinus system."

10. Running obliquely from behind forwards and downwards, a thickish column or band (e) crosses the respiratory cavity; it is hollow, and its cavity opens above and below into the sinus system. This is the "gill."

It presents an edge anteriorly and superiorly, and on each side of this, the lateral surfaces are beset with a series of small, oval, ciliated spaces. In this species the gill has but a single grand sinus running through it, and presents no appearance of vascular ramifications. The name gill has been applied to this structure somewhat too exclusively, as there can be little doubt that the whole respiratory cavity performs the branchial function. It is proposed, therefore, to call it the *hypopharyngeal* band, on the supposition that the proper respiratory cavity of the Ascidians answers to an enlarged pharynx.

11. The muscular bands (k) are closely adherent to the inner tunic; they are composed of flattened fibrils, about $\frac{1}{1200}$th of an inch in diameter, which are very distinctly transversely striated, the striæ being about $\frac{1}{7000}$th of an inch apart. The bands appear to possess no sarcolemma.

12. The intestinal canal (Plate XV. figs. 5 and 6) commences by a wide somewhat quadrangular mouth (r) opening into a flattened œsophagus, and placed at the re-entering angle formed by the hypopharyngeal band and the upper wall of the respiratory cavity. The intestine passes backwards, then becomes suddenly bent upwards upon itself, and curving slightly to the right, terminates in a wide flattened anus, close above and to the right side of the mouth (s).

A wide cæcal sac (t), given off on the left side of the intestine and bending upwards and to the right side, constitutes the stomach.

13. There is a very peculiar appendage to the intestinal canal, hitherto, it is believed, quite undescribed, and consisting of a system of delicate, transparent, colourless tubes, with clear contents, arising by a single stem from the upper part of the stomachal cæcum, and thence ramifying over the surface of the intestine (5, 6, u), on what may be called the rectum, that is, the terminal portion of the intestine; it forms a sort of expansion of parallel anastomosing vessels, which all terminate at the same distance from the anus anteriorly, and from the bend of the intestine posteriorly, either by uniting with one another or in small pyriform cæca, Plate XV. figs. 5 and 6.

Do these represent a hepatic organ, or are they not more probably a sort of rudi-

mentary lacteal system, a means of straining off the nutritive juices from the stomach into the blood by which these vessels are bathed?

The intestine is connected with the parietes of the sinus in which it lies by innumerable delicate short threads, like a fine areolar tissue.

14. In *Salpa* A, the only other organ contained in the circum-visceral sinus, besides the intestine and "system of tubes," is a mass of clear cells (*œ*), rendered polygonal by mutual pressure, and placed at the upper and back part of the sinus; to this body the name of "elæoblast" has been given by KROHN. It has by some authors been confounded with a liver, an organ to which it certainly has no analogy whatever. The elæoblast is much larger and more conspicuous in the young than in the adult *Salpæ*, and frequently, but not always, its cells contain an oily matter.

There would seem to be no clue either to the homology or to the function of this elæoblast. Without hazarding a conjecture, it may be remarked, as a curious fact, that these animals, so remarkable for possessing in the fœtal state a true though rudimentary placental circulation, possess an organ which in structure and duration somewhat calls to mind the thymus gland.

15. The nervous system consists of a single subspherical ganglion (*d*), situated in the space between the inner and outer tunics, just where the anterior and lower extremity of the hypopharyngeal band joins the ventral paries. It gives off two delicate branches forward to the "languet" (16.), and a great many in all directions to the parietes of the body. There were no branches traceable specially to the mouth or towards the œsophagus.

A delicate but strong vesicle attached to the anterior and lower surface of the ganglion, and containing four subhemispherical calcareous bodies, with black pigment spots on their outer surface, evidently represents the auditory vesicle and its otolithes in the gasteropod and acephalous Mollusca: and a conical depression in the outer tunic leading towards this auditory vesicle, would appear to be intended to bring it into closer relation with the surrounding medium, Plate XVI. fig. 5.

16. There would appear to be yet another organ of special sense, composed of the "languet" (*f*) and the "ciliated fossa" (*w*), called by ESCHRICHT the "längliches organ."

The "languet" (Plate XVI. fig. 5) is a long tongue-shaped or conical process, fixed by its base to the ventral surface of the respiratory cavity where this is joined by the anterior extremity of the gill, and for the rest of its extent floating freely in the respiratory cavity: it is curved so as to be convex anteriorly and concave posteriorly, and its anterior surface is marked by a shallow vertical groove; at the base this groove is wider, and where it becomes continuous with the surface of the respiratory cavity, it presents a narrow median slit, which leads into a small purse-shaped cavity, flattened from side to side and richly ciliated within, Plate XVI. fig. 5 *w*.

The posterior contour of this ciliated fossa is formed by a delicate thickened band or filament, much more distinct in some other species than in the present.

It would appear probable that the languet and the ciliated fossa subserve in some manner the performance of the gustatory function.

17. From each side of the base of the languet a narrow "ciliated band" (x) runs upwards, until it meets with its fellow of the opposite side, the two thus encircling the anterior aperture of the respiratory cavity.

18. The dorsal wall of the respiratory cavity is marked by two longitudinal folds, running from before backwards to the mouth. These are the dorsal folds of SAVIGNY and others; but there is an organ to which the name of "Endostyle" may be given (c), very distinct from these, and yet which has been invariably confounded with them, consisting of a long tubular filament, with very thick strongly refracting walls, Plate XV. fig. 4 c. This body lies in the dorsal sinus; its anterior extremity is slightly curved downwards, somewhat pointed, and looks stronger and more developed than the posterior extremity, which is paler, more delicate and truncated. By its ventral surface this "endostyle" is attached to a ridge of the inner tunic, which rises up into the dorsal sinus.

19. It has been stated that the circulatory system consists, not of vessels with distinct parietes, but of more or less irregular sinuses. However irregular in form, the position of several of these is very constant. There is a *dorsal sinus* running along the dorsal surface and enclosing the internal shell; there is a *ventral sinus* opposite to this and containing the ganglion; there are *lateral sinuses* connecting these. Then there is the sinus in which the intestine and generative organs lie, the *peri-intestinal sinus*, and, finally, the sinus which, connecting the dorsal and ventral system of sinuses, traverses the gill and constitutes the *branchial sinus*.

These sinuses all communicate together round the œsophagus, and above and in front of this, the heart (g) is developed. The heart lying obliquely at the posterior extremity of the dorsal sinus, is not tubular, as it has been described; it forms not more than three-fifths of a tube; nor is it correct to say that it lies in a pericardium. Its true nature will be best conceived by supposing the inner surface of a sinus to have become developed for about three-fifths of its circumference into a free muscular membrane, Plate XV. fig. 9.

This membrane is exceedingly delicate, and is composed of a single layer of flat striated muscular fibrils.

20. The direction of the circulation depends entirely upon the order of contraction of the muscular fibrils of the heart. If they contract successively from behind forwards, the blood is forced in that direction; after a certain number of such contractions, they all become simultaneously, as it were, paralysed for a short period, and then they begin to contract again, but in the inverse order, and of course with an opposite effect upon the direction of the circulation.

The blood, in its alternate flux and reflux, bathes all the internal organs—the intestine, the endostyle, the brain and the generative organs, the corpuscles finding their way as they best may among the interstices. When the force of the heart

diminishes, they frequently accumulate around the intestine in consequence of becoming entangled among the meshes of the areolar tissue (13.) connecting the intestine with the parietes.

21. So far, the structure of the two forms A and B has been identical; but in proceeding to examine the reproductive organs, it will be necessary to treat of each separately.

The form A is always found to possess a connected series of young forms, the so-called *Salpa* chain, encircling its visceral nucleus; the form B, on the other hand, never possesses the *Salpa* chain, but generally contains a solitary fœtus, pendent from the upper and posterior part of its respiratory cavity. It is clear therefore that in each of these forms reproduction takes place. But is the mode of reproduction in each case similar or different? Are both, processes of gemmation, or processes of sexual reproduction, or is one process of the one description, the other of the other description? To come at the solution of this question, it will be necessary to know first, the nature and relations of the chain of young in A, then the nature and relations of the solitary fœtus in B, and, finally, to trace back the development of both to their first origin.

22. *Salpa chain of* A (Plate XV. fig. 1 *h*. Plate XVI. fig. 1. Plate XV. fig. 9). The chain is formed of a double series of fœtuses, commencing on the right side of the nucleus, curving under it, then turning upwards and over it to the right side, and finally terminating in the middle line by a free extremity midway between the two long posterior horns.

The chain is enclosed in a proper cavity, hollowed out in the substance of the outer tunic, and this sometimes opens externally opposite the free extremity of the chain, Plate XV. fig. 9.

23. The fœtuses do not form a chain by mere apposition; they are all attached by pairs to one side of a cylindrical double-walled tube, which is connected, at its anterior or proximal extremity, with the system of sinuses of the parent, to the right of the heart. The tube is in fact merely a diverticulum of the sinus system, Plate XV. fig. 9, and the blood contained in the sinuses passes freely into it. It is divided by a partition (*y*) into two canals, which are distinct for the whole length of the tube, except at its very extremity, where they communicate just as the two scalæ of the cochlea do; and it thence happens, that in the living animal, a constant current passes upon one side of the partition and down on the other, the direction of the two currents being generally, but not always, reversed with the reversal of the general circulation.

If the fœtuses be traced back upon this tube, it will be found that towards the proximal end of the tube they lose their distinctive form and become mere buds, processes of its wall, Plate XV. fig. 9. Itmay thence be conveniently termed the "gemmiferous tube."

24. The proximal extremity of the gemmiferous tube is simply transversely striated,

Plate XV. fig. 9; further on, two elevations become apparent on either side of the median line in each of these striæ. These elevations are rudiments, the inner, of the nucleus, the outer, of the ganglion of a fœtal *Salpa*. Still more towards the distal end of the tube, the young *Salpæ* are much larger in proportion to the tube; the internal organs become marked, the heart becomes visible by its contractions, and the body itself, although the respiratory apertures are as yet only marked out, not open, contracts occasionally. Finally, the otolithes make their appearance, the body becomes larger relatively to the nucleus and ganglion, and the respiratory orifices open, Plate XVI. figs. 1, 2.

25. The cavity of the gemmiferous tube communicates with the dorsal sinus system of the fœtus. Apparently the inner canal communicates by two canals, a wider and a narrower (Plate XVI. fig. 1), with the anterior portion of the dorsal sinuses of the fœtus, and the outer canal communicates with the middle of the dorsal sinuses of the fœtus. However this may be, it is quite easy to watch the blood-corpuscles of the parent making their way from the gemmiferous tube into and out of the sinus system of the fœtuses. The writer has seen one of the large blood-corpuscles of the parent entangled in the heart (which was not more than $\frac{1}{500}$th of an inch long) of a very young fœtus.

It is not exactly true that *a gradual* series in the development of the fœtuses is to be traced along the gemmiferous tube. The tube is rather marked out into sharply-defined lengths (generally three in number), in each of which the fœtuses are nearly at the same stage of growth, while they are much further developed than in the "length" on the proximal side, much less advanced than in the "length" on the distal side.

26. In this species the young *Salpæ* thus produced were extruded, when fully developed, from the aperture mentioned in (22.); but it rarely happened that even two or three adhered together, and they never formed the remarkable free-swimming chain of other species. Generally they were found solitary, presenting only on their lateral faces traces of their former adhesion. Those which were connected adhered together in a single series, the left antero-lateral extremity of the one being applied to the right postero-lateral extremity of the other; and when they became free the traces of the connection were visible as angular processes of the sinus system.

It is not correct to say that the *Salpa* chains have organs of attachment. At first they are attached by the whole length of their lateral faces, the sinus system of one being continuous by a wide channel with the sinus system of the other; but as they grow these communicating channels become more and more narrowed until they are mere points of connection; all communication then ceases, and the *Salpæ* become free from one another and move about independently.

27. Having thus determined the nature and relations of the *Salpa* chain, it remains only to be said, that the young when freed, have a sub-ovoid, posteriorly-pointed form, five muscular bands, facetted sides, and in short are identical in form, and ultimately

in size, with the form described as *Salpa* B. One-half therefore of CHAMISSO's theory is clearly correct; *the solitary* Salpa (Salpa A) *produces the aggregate form* (Salpa B); and we may add, that this takes place by a *process of gemmation from the walls of a tube in free communication with the circulatory system of the parent.*

28. *Solitary Fœtus of Salpa* B.—Whilst this form still forms part of the chain or is but just freed, it is sure to contain a solitary fœtus; and frequently one may be found in it when it has attained its full size, but as often not.

When the solitary fœtus exists, it hangs freely in the respiratory cavity (Plate XV. figs. 4, 8) by means of a pedicle attached to the upper and posterior part of its wall, on the left side of the mouth of the parent. In its youngest and most rudimentary state it is a somewhat conical papilla (Plate XV. fig. 7) or bulging of the inner tunic, consisting of an inner oval or pyriform cellular mass, enveloped in a delicate transparent membrane, which appears to be a continuation of the inner tunic.

As development proceeds the inner mass becomes divided into two portions, a larger turned towards the respiratory cavity, and which projects more and more into it, and a smaller subspherical, turned towards and lying in the cavity of the sinus, and bathed by the parental blood.

29. The whole mass goes on enlarging, but the former portion faster than the latter. The former becomes somewhat ovate, with its long diameter in the same direction as the long diameter of the parent, and gradually assumes the form of a *Salpa*. The muscular bands, the gill, the ganglion and its otolithic sac become distinct, and eventually the heart is obviously seen pulsating close behind the pedicle of attachment, Plate XVI. fig. 6.

In the meanwhile the smaller subspherical mass has undergone a remarkable change. It has likewise become thrust from the sinus towards the respiratory cavity, so that it no longer lies in the former, but is situated in the thick pedicle of the young *Salpa*.

It has furthermore become hollow, and contains two perfectly distinct cavities or sacs; of these the outer is concave and cup-shaped and envelopes the inner, which is subspherical, Plate XVI. fig. 6 *m*. Now the outer sac is in free communication by a narrower neck, divided into two channels by a partition, with the dorsal sinus of the fœtus; and the inner sac is in equally free communication by a neck similarly divided, with a short sinus arising immediately behind the heart; and as there is no communication between the two sacs, it follows that the current of blood in each is perfectly distinct from and independent of, that in the other. A more beautiful sight indeed can hardly be offered to the eye of the microscopic observer than the circulation in this organ. The blood-corpuscles of the parent may be readily traced entering the inner sac on one side of the partition, coursing round it, and finally re-entering the parental circulation on the other side of the partition; while the fœtal blood-corpuscles, of a different size from those of the parent, enter the outer sac, circulate round it at a different rate, and leave it to enter into the general circulation in the dorsal sinus.

More obvious still does the independence of the two circulations become when the circulation of either mother or fœtus is reversed.

30. Whether this body perform the function or not, it can hardly be wrong to give it the name of a placenta. It is identical in structure with a single villus contained in a single venous cell of the mammalian placenta, except that in the Salpian placenta the villus belongs to the parent, the cell to the fœtus; the reverse obtaining in the Mammalia.

As the young *Salpa* increases in size, the placenta, ceasing to grow, becomes proportionately smaller, until the pedicle gradually narrowing the communication with the parent ceases and the fœtus becomes free, Plate XVI. fig. 3. The remains of the placenta are traceable for some time as a small diverticulum of the dorsal sinus of the young *Salpa*, Plate XVI. fig. 3 *m*.

31. The latter as it grows nowise resembles its parent. It has a prismatic form, has seven muscular bands, and developes processes from its posterior extremity. It becomes indeed perfectly similar to the form which has been described as *Salpa* A.

It thence appears that the other half of CHAMISSO's theory is also perfectly true, viz. *the aggregate form of* Salpa (Salpa B) *produces the solitary form* (*Salpa* A), and the circulatory system of the fœtus in this case is connected with that of the parent, *not immediately, but by means of a very distinct and well-developed placenta.*

Here is one very clear distinction between the two processes of reproduction. Are there any other differences? To answer this question we must proceed to trace back both processes to their origin.

32. It has been seen that the young *Salpæ* B are developed by a process of gemmation from the gemmiferous tube of *Salpa* A. Whence comes the tube itself?

The smaller the individual of the form A examined, the shorter is the gemmiferous tube, and the less developed the buds upon it. In individuals just free, or about to be free, it is a very short cylindrical tube, arising on the right side and just in front of the heart, and curving downwards and backwards, Plate XVI. figs 3, 3 *a*.

In still smaller attached specimens it appears as a very short, somewhat conical process (imperfectly divided by a partition) of the dorsal sinus, close to the heart; its walls are smooth, and the blood-corpuscles are easily seen passing up one side and down the other of the partition, Plate XVI. fig. 4.

It is clear therefore that the gemmiferous tube is nothing more than a stolon, containing a diverticulum of the circulatory system of the parent, and the whole process of reproduction as it is manifested in *Salpa* A is one of gemmation. *Salpa* B *is a bud of Salpa* A.

33. Following the same course of investigation with regard to the young *Salpa* A (which it has been seen is produced from *Salpa* B), it is found, that in *Salpæ* B, which are either still adherent to the gemmiferous tube or just set free, there is no protuberance of the inner tunic into the respiratory cavity; but where this afterwards exists, a pedicle of greater or less length is attached, and running backwards, carries

at its extremity an oval cellular mass, Plate XVI. fig. 8. This hangs suspended by its pedicle in the cavity of the sinus, and is freely bathed by the blood. In one specimen the length of the pedicle was $\frac{1}{250}$th of an inch, the long diameter of the oval body about $\frac{1}{600}$th of an inch.

In still younger forms of the *Salpa* B., and indeed as soon as the separate organs are distinguishable, the outer tunic bulges slightly in the middle line behind the outline of the posterior aperture and beneath the nucleus, Plate XVI. figs. 1, 2; this protuberance is caused by the presence of a spherical body (q) about $\frac{1}{1000}$th of an inch in diameter, containing a clear vesicle $\frac{1}{1700}$th of an inch in diameter, which again frequently contained a round opake spot or nucleus about $\frac{1}{8000}$th of an inch in diameter; the latter sometimes appeared as a thick-walled vesicle. This is plainly an ovum; a narrow pedicle (q') is attached to its upper extremity and runs upwards, curving slightly forwards to the same point as in the preceding forms.

It would appear then that the *Salpa* B developes a single ovum, which is at first placed in the median line in the ventral sinus; that partly by the increase in size of the body, and partly in consequence of a shortening of its pedicle which acts as a gubernaculum, it becomes drawn from this position upwards and to the left side; and that in the meanwhile, probably in consequence of fecundation, it becomes altered in structure, and precisely similar to and identical with the cellular mass which has been seen to form the rudiment of the young *Salpa* A, Plate XVI. fig. 7. In this case *the* Salpa A *would be a true embryo developed by a process of sexual generation.*

34. Sexual generation however presupposes a male fecundating organ, and this is found in *Salpa* B as a ramified body, hitherto generally called a liver (p), Plate XV. figs. 6 and 7, closely surrounding the intestinal canal with a network, solid in the younger form, but in the older tubular, with very thin walls, and containing a vast number of pale-greenish circular cells, from $\frac{1}{5000}$th to $\frac{1}{1700}$th of an inch in diameter; and besides these detached spermatozoa, with very thin tails and long narrow heads, about $\frac{1}{1600}$th of an inch in length. The testis had no visible excretory organ, but such might well escape notice.

Nothing at all resembling this body is found in the form A; its contents sufficiently demonstrate its real nature, and its existence on the other hand is strong confirmatory evidence, if any be needed, that the pediculate body described above is a true ovum.

One curious circumstance needs to be remarked; the testis does not develope *pari passu* with the ovum and attain its full development at the same time, as might be imagined. The testis is always behind the ovum in its progress, and does not, indeed, seem to have attained its full development until the latter has become freed from the parent.

Without carefully tracing the form B through all its stages, it might readily be supposed to be always male; in fact, fully-grown specimens, while they always possess

a well-developed testis, rarely contain any embryo, this being generally set free when the parent is about half or two-thirds grown. The careful observer will, however, be always able to detect a trace of its former attachment, in a sort of cicatrix, left at the corresponding part of the respiratory chamber.

35. It is not clear by what channel fecundation takes place, whether each *Salpa* B impregnates its own ovum by discharging the contents of its own testis into the circulatory fluid, which would be a procedure altogether anomalous; or whether, on the other hand, impregnation do not rather take place from without, a presumption which is strengthened by analogy, and by the fact, that the testis does not seem to attain maturity early enough to fecundate its own ovum. The spermatic fluid may have access to the ovum by the gubernaculum becoming hollow and tubular, as will be seen to be the case in the *Pyrosomata*, and indications of such an occurrence have occasionally manifested themselves.

36. To recapitulate.—The form A (*Salpa solitaria*) produces a stolon, from which, by gemmation, arises the form B (*Salpa gregata*). This contains a testis and a single ovum attached by a pedicle or "gubernaculum" to the wall of the respiratory chamber. Fecundation takes place in a manner not yet clearly ascertained, and the "gubernaculum" shortens until the ovum is brought into close contact with the respiratory wall or inner tunic. The latter then protrudes into the respiratory canal, enveloping the ovum in a close sac; the ovum becomes developed into an embryo, which is connected by a genuine placenta with its parent, and ultimately assuming the form of *Salpa* A becomes detached and free.

37. While CHAMISSO's formula, then, expressed the truth with regard to the generation of the *Salpæ*, it did not express the whole truth.

True it is, that the *Salpa solitaria* always produces the *Salpa gregata*, and the *Salpa gregata* the *Salpa solitaria*; but it is most important to remember that the word "produce" here means something very different in the one case, from what it means in the other. In the *Salpa solitaria* the thing produced is *a bud*; in the *Salpa gregata a true embryo*. There is no "alternation of generations," if by generation sexual generation be meant; but there is an *alternation of true sexual generation with the altogether distinct process of gemmation.*

It would be irrelevant to discuss here the wide question of the "alternation of generations" in all its bearings; but the writer may be permitted to express his belief, founded upon many observations upon the Polypes, Acalephæ, &c., that the phenomena classed under this name are always of the same nature as in the *Salpæ*; that under no circumstances are two forms alternately developed by *sexual generation*; but that wherever the so-called "alternation of generations" occurs it is *an alternation of generation with gemmation.*

38. Using the terminology of insect metamorphosis, as CHAMISSO has done (70.), the larva never produces the imago by sexual generation, the imago again producing the larva by sexual generation. But a pseud-imago, which is indeed nothing more,

homologically, *than a highly individualized generative organ*, is developed from the larva, ova are produced by it, and from these the larva again is developed; the whole process differing from that common to animals in general, in nothing but the independence and apparent individuality of the generative organ.

39. It cannot be too carefully borne in mind that zoological individuality is very different from metaphysical individuality, and that the whole question of the propriety of the "alternation theory" as a means of colligating the facts (for at best it can be nothing more) turns upon the nature and amount of this difference.

If the true definition of the zoological individual be (as the writer believes it to be) "the sum of the phenomena successively manifested by, and proceeding from, a single ovum, whether these phenomena be invariably collocated in one point of space or distributed over many," then there is no essential difference between the reproductive processes in the higher and lower animals, and the alternation theory becomes unnecessary.

In accordance with this definition, neither the form A, nor the form B would be a zoological individual; not either of their forms, but both together, answer to the "individual" among the higher animals.

In strictness both *Salpa* B and *Salpa* A are only parts of individuals,—are organs; but as we are unaccustomed to associate so much independence and completeness of organization with a mere organ, to give them such a name would sound paradoxical. It is proposed therefore to call them, and all pseudo-individual form resembling them, "zoöids," bearing in mind always that while the distinction between zoöid and individual is real, and founded upon the surest zoological basis,—a fact of development,—that between zoöid and organ is purely conventional, and established for the sake of convenience merely*.

40. In the *Salpæ*, then, the parent and the offspring are not dissimilar, but the individual is composed of two zoöids.

In *Cyanea*, the individual is composed of two "zoöids," a medusiform and a polypiform zoöid.

In the *Trematoda* there are frequently three "zoöid" forms to the individual.

In the Aphidæ the sum of from nine to eleven "zoöids" composes the individual, the great number of zoöid forms in this case being simply an instance of that "irrelative repetition" of parts so common among the lower animals.

A similar irrelative repetition exists among the so-called "compound" animals, the Polypes and compound Ascidians; and consistently with the present theory we must call a *Sertularia* or a *Pyrosoma*, for instance, not an aggregation of individuals

* For a further consideration of this subject the author begs to refer to Dr. CARPENTER's "Principles of Physiology," in which the whole question of individuality in plants and animals is treated in a very clear and masterly manner; to Mr. THWAITES's papers in the Annals of Natural History; and to an attempt to apply the principles advocated in the text to the metamorphosis of the Echinoderms in a Report by himself.—*Annals*, July 1851.

into a common mass, but an individual which is developed into a greater or less number of zoöid forms, which in the present case remain united.

Thus the stem and branches of the polypidom in *Sertularia* are "organs," the ovarian vesicles are "organs," the polypes are "zoöids;" the sum of the organs and zoöids constitutes the individual.

If the separate polypes be individuals, what is the polypidom which exists before them, and therefore cannot be derived from them?

It seems startling to assert that a *Salpa* of the form A with some fifty or sixty of the form B which proceed from it, constitutes but one zoological individual; still more to aver this of some millions of Aphides all proceeding indirectly from one ovum; but these difficulties have reference merely to our ordinary notion of individuality, and involve us in no self-contradictions and inconsistencies such as seem inherent in any other view of the case.

SECTION II.—*The Anatomy of* Pyrosoma.

41. This genus, first established and very imperfectly described by PERON*, received elaborate investigation from LESUEUR† and from SAVIGNY‡, who very carefully described every part of its organization with the exception of the generative organs, and one or two other points of minor importance.

Subsequently M. MILNE-EDWARDS§ showed that the nature of the circulation was the same in it as in the other Ascidians.

Of the three species distinguished by LESUEUR the present appears most closely to resemble the *P. atlanticum*.

42. The only specimen of this remarkable animal which the writer has had an opportunity of examining in the fresh state, was procured on the night of the 15th of June 1850, in about 45°·85 S. lat. and 110°·30 W. long. The sky was clear but moonless, and the sea calm; and a more beautiful sight can hardly be imagined than that presented from the decks of the ship as she drifted, hour after hour, through this shoal of miniature pillars of fire gleaming out of the dark sea, with an ever-waning, ever-brightening, soft bluish light, as far as the eye could reach on every side. The *Pyrosomata* floated deep, and it was with difficulty that some were procured for examination and placed in a bucketfull of sea-water. The phosphorescence was intermittent, periods of darkness alternating with periods of brilliancy. The light commenced in one spot, apparently on the body of one of the "zoöids," and gradually spread from this as a centre in all directions; then the whole was lighted up; it remained brilliant for a few seconds, and then gradually faded and died away, until the whole mass was dark again. Friction at any point induces the light at that point, and from thence the phosphorescence spreads over the whole, while the

* Annales du Museum, 1804.

† Journal de Physique, 1815.

‡ Mem. sur les Animaux sans Vertèbres.

§ Comptes Rendus, 1840.

creature is quite freshly taken; afterwards, the illumination arising from friction is only local.

43. So far as could be observed the *Pyrosoma* had no power of locomotion; any such power arising from a contraction of the hollow cylinder is out of the question, as its substance is cartilaginous and non-contractile. Any one who does not examine these animals quite closely may be readily deceived on this point; for the alternate fading and brightening of the phosphorescent light gives rise to the impression that the creature recedes from and approaches the eye; and viewing them from the deck of a ship only, it is difficult to imagine that they do not really move with some rapidity*.

44. The *Pyrosoma* may be described as a hollow cylinder, solid and hard to the touch, closed and rounded at one end, open at the other. A narrow lip projects inwards at the open extremity; it has been called a membranous diaphragm, but in the specimen examined it was certainly cartilaginous and immoveable, like the rest of the animal. The thickness of the wall of the cylinder was about two-fifths of an inch; its diameter was about 1 inch and a half; its length was about 10 inches. The outer surface of the cylinder was covered with a multitude of small projections, and close to them opened small circular apertures. The inner surface of the cylinder was uneven but not rough, and was similarly pierced with circular apertures.

The wall of the cylinder consists of a vast number of minute Ascidian "zoöids" lying perpendicular to the axis of the tube, and united together by a common cartilaginous basis; and the small circular apertures correspond respectively, the outer to the anterior aperture of the *Salpa*, the inner to the posterior aperture.

Each aperture is provided with a small dentated membranous valve, Plate XVII. fig. 1.

45. In each zoöid there is at one point a ganglion (*d*), with a mass of deep red otolithes. As in *Salpa*, this must be called the ventral side; the opposite is the dorsal side, and contains (as in *Salpa*) an endostyle, Plate XVII. figs. 1, 2 *c*. The ganglionic or ventral surfaces of all the polypes are turned the same way, and towards the open end of the cylinder.

By far the greater part of the space occupied by each zoöid is taken up by the respiratory cavity. This is elliptical, and compressed laterally. It is lined by the proper branchial network, hereafter to be described (*v*), and communicates freely by means of the apertures in the branchial network with the post-branchial or anal cavity, which, as before stated, opens into the interior of the cylinder.

46. The viscera lie behind the branchiæ. They consist of the digestive canal, heart, and generative organs.

* My observations upon the power of locomotion of *Pyrosoma* were very imperfect, as I was anxious rather to attend to the more interesting points of structure. Certainly the cylinder does not contract as a whole, but it is very possible that the zöoids do, and so move by the reaction of the forced-out water against the closed end of the cylinder.

The intestine (r, s, t) commences by a wide mouth with thick lips, at the posterior, ventral extremity of the respiratory cavity. The œsophagus (r) runs back, and then upwards to terminate in the wide subquadrilateral stomach (t). A narrow pylorus communicates with the intestine, which passes at first upwards and forwards, and then suddenly becoming bent upon itself, runs downwards and to the right side, to end in the wide flattened anus (r).

The œsophagus is dotted over with branched carmine pigment-cells; and similar cells are frequently seen upon the intestine just beyond the pylorus.

47. A tubular axis (u) arises from the stomach, and branches out on the rectum into a system of tubes as in *Salpa*; but the ramifications are less numerous and less regular, with wider meshes than in the latter. The tubes are less transparent and have more the appearance of solid fibres, and finally they terminate towards the anus in wide globular cæca.

The stem of this system is about $\frac{1}{1200}$th of an inch in diameter.

48. Each zoöid is composed of two tunics, an outer (α), confluent with the general cartilaginous basis, and an inner (β), continuous with the outer at its anterior and posterior extremities, and adherent to it antero-laterally, in two oval spots, one on each side, which, when examined by the microscope, appeared to consist of nothing more than an aggregation of clear circular cells about $\frac{1}{800}$th of an inch in diameter. (δ). These were considered by SAVIGNY to be the ovaria, but they have not the appropriate structure, and it will be seen that the ova are formed elsewhere.

In all the rest of their extent the inner and outer tunics are separated by a very obvious space. This is one large vascular sinus, and the viscera lie in it and are bathed by the blood which fills it.

The heart (g) is placed on the dorsal side just behind the posterior extremity of the internal shell. In structure it perfectly resembles that of *Salpa*, and its contractions are reversed in a similar manner. No distinct vessels were to be traced in these animals.

49. The endostyle (c) resembles that of *Salpa* in its structure. It is as long as the branchial chamber, and lies in the dorsal sinus, supported by a projecting ridge of the inner tunic. On each side of it below, there is a longitudinal thickening, which readily gives rise to the appearance of four dorsal bands or "undulated vessels," described by SAVIGNY.

50. The branchiæ (v) are symmetrical, one on each side, and are composed of a network formed by longitudinal and vertical bars or laminæ.

The vertical bars are outside; the longitudinal bars are at equal distances along their inner surface, and are attached at the point of intersection.

The vertical bars are attached to the inner tunic at their upper and lower extremities; for the rest of their extent they are free.

The longitudinal bars (v, fig. 3) are rather laminæ, flattened horizontally, slightly thickened at their free edges, and beset along the upper surface of these

edges with small teeth; they project anteriorly and posteriorly beyond the vertical bars.

Both systems of bars appeared to be tubular, although no corpuscles were seen moving in them, and the edges of the vertical sinus were thickly covered with long cilia, moving in opposite directions on the opposite sides.

51. The dorsal edges of the two branchiæ were separated by a space containing the thickened dorsal folds already mentioned, and this is continuous posteriorly with a band which connects the mouth with the dorsal surface of the respiratory cavity, and allows the water to pass back on each side of it to the post-branchial cavity.

52. Anteriorly on the ventral side is an organ (fig. 10 *w*) analogous to the "ciliated fossa" of the *Salpæ*, and behind this a series of tongue-shaped eminences (fig. 1 *f*) projects into the respiratory cavity, analogous to the "languet" of the *Salpæ*.

The "ciliated fossa" is compressed laterally, and placed upon the upper surface of a protuberance, formed by the ventral wall of the respiratory cavity in the middle line. On each side a flattened ciliated band (fig. 10 *x*) runs up on the respiratory wall in front of the anterior edge of the branchiæ, and meets above with its fellow of the opposite side.

The "languets" are altogether eight in number. They extend in a longitudinal series between the ciliated fossa and the mouth. They are all slightly excavated and ciliated anteriorly.

53. Immediately beneath the ciliated fossa, and in the midst of the ventral sinus, lies the ganglion. This is about $\frac{1}{146}$th of an inch long, somewhat egg-shaped, with its large end forwards. Its posterior extremity is in contact with a mass of deep red otolithes, fig. 10 *d*.

A small nerve runs from the ganglion to the lateral ciliated band. Five or six branches are distributed to the anterior aperture, and two principal branches run backwards to the posterior aperture, giving off branches to the mouth in their course.

54. The *Pyrosomata* are hermaphrodite.

The testis (*p*) is the so-called "hepatic organ" of LESUEUR, SAVIGNY and PERON. It consists of ten, twelve, or more cæca, connected by their posterior extremities, and here joining a central duct, which opens by a papilla at the upper and posterior part of the respiratory cavity. The spermatic sacs lie loosely in a dilatation of the vascular sinus, and are bathed freely by the blood.

Each sac is delicate and thin-walled, about $\frac{1}{500}$th of an inch in diameter, and very variable in length. In adult specimens the distal or anterior end of each sac is filled with a pale cellular mass. Towards the attached end this becomes darker and more distinctly granulous, and the filiform bodies of masses of spermatozoa are plainly perceived.

The spermatozoa have narrow elongated heads and very long delicate tails.

55. There cannot be said to be any ovary properly so called. But to the left, and

rather in front of the testis (fig. 5), there could always be found more or less decided traces of one or more ova.

Commonly there was a single ovum (figs. 4–6), measuring about $\frac{1}{230}$th of an inch in diameter, with a clear germinal vesicle $\frac{1}{600}$th of an inch in diameter, and a vesicular thick-walled germinal spot $\frac{1}{1600}$th of an inch in diameter.

The ovum is inclosed in a strong transparent sac, continuous with a pedicle or gubernaculum (fig. 6 q'), which runs to the upper and posterior part of the inner tunic on the left side, and there terminates in a papilla, like that of the vas deferens, projecting into the post-branchial cavity.

In young specimens, when the ovum is small and the yelk pale, this gubernaculum frequently appears to be solid; but in fully-grown specimens, when the ovum has its full size, and the yelk is darker and granulous, it presents the appearance of a wide tube, especially at its upper part. And here there was frequently an appearance of dark striæ and moving granules, prompting the belief that spermatozoa had travelled thus far.

In one instance (fig. 6) the sac of the ovum was empty and the gubernaculum or duct widely distended. The appearance of spermatozoa in the duct was here very strong, fig. 5.

None of the compound ova described by SAVIGNY were present in the specimens of *Pyrosoma* examined.

56. The young polypes described by SAVIGNY as existing between the fully-formed ones, in all stages of development, are formed by gemmation, Plate XVII. fig. 7 *q*.

A diverticulum of the dorsal sinus of the parent is formed just above the heart; the extremity of this diverticulum thickens and enlarges, and assumes the form of a single zoöid. For a long time a vascular connection is maintained between it and the parent, by means of a duct, in which there seemed to be traces of a longitudinal partition, as in the gemmiferous tube of *Salpa*. Ultimately the connection appears to cease, and the two polypes live on independently.

It is to be remarked, that while in *Salpa* the ventral side of the young bud is first marked out, and the communication of the parent with the young is thence on the dorsal side of the fœtus, in *Pyrosoma* the dorsal side is first developed, and the communicating canal opens on the ventral side of the young.

57. The ovum or ova, for there are sometimes two or three, are perceptible very early in the young polype produced by gemmation, and are then situated in the middle line posteriorly.

58. The muscular system is best seen in a young specimen (fig. 8 *k*). Two very delicate bands encircle the inner tunic anterior to the ganglion. From the posterior extremity of the ganglion two strong bands arise, which diverge for about half the distance between the ganglion and the mouth. Here they divide into two branches, one of which continues the original direction, while the other meets its fellow just behind the mouth. The former, as it leaves the under surface to become lateral, is

much increased in size, and eventually terminates at a short distance from the generative glands, forming on each side the band of which SAVIGNY speaks as passing towards the liver.

Midway between the ganglion and the point of division, the diverging bands give off each a thin band, which runs to the lateral oval cellular masses.

SECTION III.—*The Homology of Structure of* Salpa *and* Pyrosoma, *and of these with the ordinary Ascidians.*

59. It seems to have been pretty generally admitted by naturalists, that the *Tunicata* are susceptible of division into two great classes, the Monochitonida and Dichitonida, characterized by certain differences in the structure of the branchiæ and in the degree of adhesion of the inner and outer tunics.

Of the two species whose structure has been described, *Salpa and Pyrosoma,* the former was placed among the Monochitonida (or " those having the inner sac adherent throughout to the outer tunic"), while the latter was reckoned among the Dichitonida (or those " whose inner sac is adherent to the outer tunic, at its two orifices, only").

Now there is an ambiguity which must be noticed here at starting, as it is one which has caused much confusion, and must, unless cleared up, cause our conception of the real structure of the Ascidians to be very indistinct. Authors speak of the greater or less adherence of the outer and inner sacs, and consider the " outer sac" of the ordinary Ascidian to be homologous with the outer tunic of the *Salpa.* The " inner sac," again, is with them homologous with the inner tunic of the *Salpa.* But it is not so; every Ascidian, as M. MILNE-EDWARDS has clearly shown in *Clavelina,* consists of three tunics: an outer, the *test*; a middle, which is here called outer *tunic*; and an inner, the inner *tunic.* The inner tunic of the *Salpa* answers to the inner tunic of *Clavelina,* but its outer tunic answers to the test and the outer *tunic* together (90.)*.

However, with regard to the two genera in question, whatever be the nature of the two membranes of which they are composed, there is absolutely no distinction whatever to be drawn between them. The inner membrane is just as much or as little adherent to the outer in *Pyrosoma* as in *Salpa.* In each case the wide sinuses between the two membranes form the sole vascular system.

60. It may be said that there is an essential difference between *Salpa* and *Pyro-*

* This essential difference between the test and the two *tunics* of the Ascidians has its origin in the embryo. The tunics are formed by the ordinary process of development, while the test having a totally different chemical composition, is in a manner secreted round, and envelopes the whole embryo.

There seems to be a certain independence in the mode of growth of the embryo and that of the test, the former lying at first quite free in the latter; and it appears to depend entirely upon the relative rates of growth of the two whether the resulting Ascidian shall be Monochitonidous or Dichitonidous.

The test of the Ascidian composed of cellulose is every way homologous with the test of the Mollusk composed of carbonate of lime.

soma in the structure of the branchiæ. A little consideration, however, will show that this is merely a difference in degree.

SAVIGNY has shown that in certain *Salpæ* there is an upper division of the "gill," an "epipharyngeal band" (to carry out the nomenclature adopted at (10.)), as well as a hypopharyngeal band.

Now in the genus *Doliolum* (88.)* this epipharyngeal band has attained a much greater development (though the mouth still remains at the upper part of the cavity), and like the hypopharyngeal band carries a number of ciliated branchial bars. These bars have a direction more or less parallel to those carried by the hypopharyngeal band, and hence there appear to be two branchiæ, an upper and a lower†.

But in *Pyrosoma* the mouth is on the ventral side of the animal; the epipharyngeal band, developed in proportion to the distance of the mouth from its normal position, takes a direction at right angles to the axis, and thence comes to carry the branchial bars belonging to it parallel to the axis; while the hypopharyngeal band carrying its branchial bars as before, the two sets cross and produce the branchial network.

The line between the Monochitonida and Dichitonida then can certainly not be drawn between the *Salpæ* and *Pyrosomata.*

61. The *Pyrosomata,* in the main, have the closest similarity in structure to the Botryllidæ and other compound Ascidians; but in these latter, the separation between the test and the outer tunic becomes more and more marked, until it attains its greatest amount in the Clavelinidæ, Cynthiæ, &c.

Now does this separation furnish a character of any value or importance, systematically? Surely not, for the value of a character depends upon the number of differences of which it is a mark; and this is the mark of none.

SAVIGNY observed the close resemblance between *Botryllus* and *Pyrosoma,* which yet differ in this character.

Clavelina and *Perophora* are acknowledged to be closely allied genera, and yet in the former the test and outer tunic are separated to their utmost extent; in the latter‡ they are as closely united as in any *Salpa.*

In the Cynthiæ the test and tunics are generally very distinct; but in *Cynthia ampulloides,* judging by the descriptions of VAN BENEDEN, they are confounded together§.

Again, in the *Salpa vaginata* of CHAMISSO, the test makes its appearance as a

* And it may be added in the genus *Anchinaia,* described in WIEGMANN's Archiv for 1833, which seems to be a most interesting transition form between the *Salpæ* and *Doliolum,* if indeed it be not the young form of *Doliolum caudatum* itself.

† See also on the homology of the branchial organs of the *Salpæ* and ordinary *Tunicata,* M. MILNE-EDWARDS, Sur les Ascidies composées, p. 55.

‡ See the very beautiful figures and descriptions of LISTER in the Philosophical Transactions for 1834.

§ Mém. de l'Acad. Roy. de Bruxelles, tome xx.

separate structure, and the cavity in which the gemmiferous tube lies in all the *Salpæ*, and through which it makes its way to the exterior, seems to represent the normal separation of the test and tunics.

The homology of the cellulose test of the Ascidian with the calcareous test of the Mollusk has already been adverted to; and it would seem that the separation of the former from the tunics, or its confusion with it, is of as little value as a character among the *Tunicata*, as the imbedding of the shell in the mantle in *Limax* would be in separating it from *Helix*, whose shell is distinct from the mantle.

62. It would appear, indeed, that in no natural family is it less possible to draw any very broad line of demarcation among the various members than in the *Tunicata*.

Tracing them one by one, we find that all the organs of the *Salpæ* have their homologues among the other Ascidians; the various genera passing one into the other by almost imperceptible gradations.

Even the connection of the fœtus with the parent by a placenta, a feature apparently so unique in the *Salpæ*, seems to be not without its analogue in the Didemnidæ*.

The actual fact of a placental circulation indeed has not been observed, but it may be surmised, as M. MILNE-EDWARDS† has observed the ova to be developed within a diverticulum of the vascular system of the parent.

The peculiarly formed heart, the circulation without distinct vessels, and the reversal of its direction are common to all *Tunicata*.

63. In all the *Tunicata*, again, it would seem that the first bend of the intestine (whatever its subsequent course) is dorsal, *i. e.* to the side opposite the ganglion, and almost always to the right side. *Doliolum*, however, seems to be a sinistral *Tunicate*.

What has been described in the present paper as the "Tubular System" was found by LISTER (Philosophical Transactions, 1834) in *Perophora*, and described by him as "transparent vessels that may be supposed lacteals."

In *Chelyosoma* there is a mass of otolithes and a fossa, seemingly analogous to the "ciliated fossa."

The "languet" of the *Salpa* has its homologues in *Pyrosoma*, *Chelyosoma* and *Clavelina*, and is represented by smaller tentacular filaments in *Cynthia*, *Diazona*, *Synoicum* and *Polyclinum*.

64. All the *Tunicata* are hermaphrodite; and from the small size of the only efferent

* The only remaining important difference of *Salpa* from its congeners consists in the *Salpa* larvæ being tailless, while, as the beautiful researches of M. MILNE-EDWARDS have shown, the other Ascidian larvæ have tails. This exception, however, is singularly paralleled among the Amphibia. The larvæ of the ordinary Amphibia have, as is well known, deciduous tails like the ordinary Ascidians. *In the genus* Pipa, *however, which carries its young in cells upon its back, the larva is tailless.* (LEUCKART, Ueber Metamorphose, &c. SIEBOLD and KÖLLIKER's Zeitschrift für Wissenschaftliche Zoologie, 1851.) Such a veıy striking analogy needs no comment.

† Obs. sur les Ascidies composées, p. 23.

generative duct in the Botryllidæ, it would seem that the ova make their exit in the same way as in the *Salpæ*.

All the *Tunicata* possess the power of gemmation, and the buds are always formed as in *Salpa* (though not always with the same regularity), from a diverticulum of the sinus system.

65. With regard to the "endostyle," which appears hitherto to have been strangely confounded with the dorsal folds of the inner tunic, the writer can speak positively as to its existence in the *Salpæ*, *Pyrosomata* and certain Botryllidæ. In all these species it is figured by CUVIER, CHAMISSO, SAVIGNY and MILNE-EDWARDS*, but not described; and as a precisely similar structure is figured by SAVIGNY and others in the solitary Ascidians, it is not perhaps too much to assume that the endostyle exists in them also. Should such be the case, we should be furnished with a new and very remarkable distinctive character of the *Tunicata*†.

The "elæoblast" of the *Salpæ* appears to be represented in the solitary Ascidians by the calcareous mass in contact with the heart, described by VAN BENEDEN in *Cynthia ampulloides*.

66. The simple epipharyngeal and hypopharyngeal bands of the *Salpa* have been traced through their first degree of complication in *Doliolum* to *Pyrosoma* and *Botryllus*, where they form a true branchial sac, differing from that of the simple Ascidians only in the number and size of its meshes.

On the other hand, in *Pelonaia* the hypopharyngeal band itself has disappeared. It is a *Salpa* in which the oral and cloacal orifices have approximated while the "gill" has become obliterated‡.

In the strange form *Appendicularia* (79.), the simplification is carried a step further, for there is but one orifice, the oral. The anus opens on the dorsal surface, and a long appendage is added in the same position as that of *Boltenia*, but instead of being a long pedicle of attachment, it is a free and energetically moving fin.

67. To sum up what has been said, it appears that the *Salpæ* are not, as has been generally supposed, an aberrant form of the *Tunicata*, but rather that they are connected by insensible gradations with the other forms of the group; neither is there any circumstance in their two modes of multiplication at all at variance with what takes place in other genera of the family.

The distinction between monochitonidous and dichitonidous *Tunicata* cannot be kept up in its present sense, for the proper inner and outer tunics are equally adherent in all *Tunicata*; and as expressing the degree of adherence of the test to the

* LISTER, in his description of *Perophora, loc. cit.*, figures the endostyle and says, "along the middle of the back is a vertical compound stripe, *d* (fig. 4), that seemed to me cartilaginous."

† Since the above was written the author has had the satisfaction of finding both the endostyle and the ciliated sac, in a small, very transparent *Cynthia* (—— ? sp.) obtained at Felixstow, on the Suffolk coast.

‡ *Chelyosoma* would appear to resemble *Pelonaia* in the absence of any distinct branchial sac; but ESCHRICHT's figures are not very clear.

outer tunic, the distinction is of no value, systematically, as the character may vary greatly in the same or closely allied genera.

SECTION IV.—*History of our Knowledge of the* Salpæ.

68. FORSKAHL, the Danish naturalist, founded the genus *Salpa* upon certain animals taken in the Mediterranean. No less than eleven species are described and figured by him (and with remarkable clearness and accuracy) in his "Descriptiones Animalium," a work which he unfortunately did not live to see published, but which made its appearance in the year 1775.

The following is his definition of the genus: "Salpa corpore libero, gelatinoso, oblongo, utroque apice aperto; intus vacuo; intestino obliquo variat: *a*) nucleo globoso, opaco, juxta anum *b*) nucleo nullo sed linea dorsali opaco.

"Nomen mutuatum a Σάλπα, pisce a Græcis cognito et huic vermi additum ob similitudinem formæ cum tubo canoro. Animal plerumque gregarium; mira cohærens symmetria motum corporis per systolem et diastolem, siphonica arte perficiens."

BROWNE*, who appears to have been unacquainted with FORSKAHL's work, gave the name of *Thalia* to some *Salpæ*, which he describes and figures in the rudest manner.

BOSC seems to have been the first to suspect the identity of these two genera, a suspicion which was converted into a certainty by the researches of CUVIER, who not only disentangled the nomenclature of the genus from the confusion into which it had fallen, but gave the first accurate idea of the anatomy of the *Salpæ*, and first announced their true zoological relations.

69. Much was added piecemeal to the foundation thus laid by CUVIER, by subsequent authors. MEYEN and MILNE-EDWARDS described the nervous system, KUHL and VON HASSELT, ESCHSCHOLTZ and MILNE-EDWARDS, announced the singular nature of the circulation. CUVIER and CHAMISSO hinted, and MEYEN described, the placental connexion of the solitary fœtus with the parent; ESCHRICHT and SARS declared the proximate nature and mode of origin of the *Salpa* chain.

70. CHAMISSO again founded the theory of the "alternation of generations," using that very phrase† to express the peculiarities accurately observed by him in the mode

* Natural History of Jamaica, 1785.

† Justice seems to have been hardly done to CHAMISSO as the first promulgator of the theory of the "alternation of generations." He says at p. 10, "Qua seposita (Salpâ bicorni) *alternationem generationum* legem esse ut posuimus genericum, omnibus communem speciebus, observationibus innititur;" and at p. 3, "Talis speciei metamorphosis generationibus in Salpis duabus successivis perficitur, *forma per generationes* (*nequaquam in prole seu individuo*) *mutata*. Verum enimvero qua lege proles Salparum, ut animal ab ovo, imago a larva, inter se differunt, parum elucet." And in his interesting "Reise um die Erde," CHAMISSO shows still more clearly his distinct conception of the theory by the remarkable phrase, "Es ist als gebäre die Raupe den Schmetterling und der Schmetterling hinwiederum die Raupe." "It is as if the Caterpillar brought forth the Butterfly, and the Butterfly the Caterpillar."

Subsequent writers seem not to have done much more in reality than bring new cases under the law here so

of multiplication of the *Salpæ*, but the nature and existence of the sexual organs remained undetermined until KROHN and STEENSTRUP in 1846 discovered the male organs; subsequently KROHN made out the true ovaries also.

Finally, a most accurate account (to which indeed the present memoir can be considered only as confirmatory independent testimony) of the whole course of development and reproduction of the *Salpæ* was given by KROHN in the Annales des Sciences for 1846.

71. Without undertaking the somewhat unprofitable task of giving a detailed historical account of all that has been written upon the *Salpæ*, it may be of interest to notice, with a view to reconcile, a few of the more important discrepancies among the statements of the chief investigators. And first:

Of the sides and ends of the Salpæ.—On so simple a matter as this, almost every writer has different views. CUVIER calls the ganglionic surface ventral, the opposite dorsal, the nuclear end anterior, the opposite posterior. SAVIGNY appears to follow him. CHAMISSO follows CUVIER as to the anterior and posterior ends, but reverses the dorsal and ventral sides.

MM. QUOY and GAIMARD give the ganglionic end as anterior, the nuclear as posterior, the nuclear side as ventral, the ganglionic as dorsal.

MEYEN gives the same determination. ESCHRICHT considers the nuclear end to be posterior, the ganglion side ventral; as also SARS.

M. MILNE-EDWARDS seems to follow CHAMISSO. It is much to be wished that some uniform nomenclature could be adopted. The reasons for the terms used in the present paper have already been given (5.).

72. *The Nervous System.*—The nervous system was denied by CUVIER altogether. SAVIGNY describes the ganglion, without recognizing its true nature, as the "tubercule qui dans les Ascidies est contigu au gros ganglion."

CHAMISSO describes what appears to be the thickened edge of the "ciliated fossa," and states that ESCHSCHOLTZ considered it to be a nerve (*op. cit.* p. 5).

QUOY and GAIMARD describe the ganglion, but omit all mention of the auditory sac.

MEYEN claims the discovery of the true nervous system; but although he figures it pretty accurately, he omits all mention of the otolithic sac, and seems after all in doubt whether it may not be a respiratory organ; and it was reserved for M. MILNE-EDWARDS to give the first satisfactory account of these structures.

Both ESCHRICHT and SARS subsequently omit to describe the auditory sac.

clearly expressed, and they do not always seem to have kept so clearly in mind the modest renunciation of any claim on the part of the theory to be an *explanation* of the facts, contained in the last paragraph of the former quotation.

Finally, it must not be forgotten, that though CHAMISSO was the first promulgator of the "alternation," he expressly (with a candour impossible to be too much commended) gives the credit of the conception to his companion ESCHSCHOLTZ, "generationis Salparum primus et perspicax fuit indagator amicissimus ESCHSCHOLTZ," p. 9, and again in the preface to the second fasciculus of his observations.

73. *The "Ciliated Sac" and "Languet."*—CUVIER refers to this organ in *Salpa Tilesii* as "l'anneau irregulière qui la termine (la branchie) en arrière."

It has already been mentioned that this organ is mentioned by CHAMISSO as a problematical nervous apparatus. QUOY and GAIMARD described its thickened rib as a vessel, adding, "nous dirons un vaisseau parceque nous croyons avoir vu le sang circuler dans son intérieur," apparently mistaking the ciliary motion for a circulation.

MEYEN calls it the "Respirations-ring," and says that it is a respiratory organ. He first described the cilia, but denies the existence of any aperture leading into the organ.

In *S. mucronata*, not perceiving that he has to do with the very same organ under a different form, he describes the "ciliated sac" as a testis. The languet he calls simply "Haken."

ESCHRICHT gives it and the languet together, the name of "das längliche organ," and considers it as a tactile organ analogous to the pulps of bivalves. He rightly describes the nervous cords connecting it with the ganglion.

SARS confirms ESCHRICHT's view, and considers the organ as analogous to the tentacles of the Ascidians, which, however, cannot be the case, as in many Ascidians (e.g. *Clavelina*) the tentacles and the "languets" co-exist*.

M. MILNE-EDWARDS figures the "ciliated fossa" as the "fossette prébranchiale" in the plates of the last (commemorative) edition of CUVIER's 'Règne Animal.'

74. *The Structure of the Heart.*—ESCHRICHT and SARS describe the heart to be composed of a series of vesicles, which is certainly a mistake, arising from the fact that the heart always presents two or three constrictions, so as to appear almost moniliform.

75. *Tubular System.*—This is figured by MM. QUOY and GAIMARD (pl. 88, fig. 12) in *Salpa pinnata*, under the name of "vaisseaux mésenteriques." Is it to this structure to which M. KROHN refers, when he says that "the meshes or lamellæ of the elæoblast are traversed by numerous vessels opening into two trunks, which apparently form the attachment between this organ and the visceral nucleus?"

Perhaps also it is to this system that ESCHRICHT refers when he speaks of the intestine as beset with "stalked granules."

76. *The Gemmiferous Tube.*—CUVIER, SAVIGNY, CHAMISSO and QUOY and GAIMARD consider this structure as more or less partaking of the nature of an ovary.

MEYEN mistakes it for a liver in *Salpa democratica*. ESCHRICHT describes the process of development of the young from the gemmiferous tube and their connection with it very carefully; but he does not seem to consider it as mere gemmation.

He calls the organ "Keim-röhre," germ-tube, and considers it as a "quite new form" of propagative organ. From the mode of expression in the following para-

* In the *Cynthia* examined by the author (see note (65.), the "ciliated sac" was seated upon a tubercle, but there was no "languet."

graph he evidently thinks the propagation here to be in some manner sexual. "Die Eintheilung in Strecken deren jede Fötus von einerlei Ausbildung enthält, deutet allzu bestimmt auf verschiedene Befruchtungen hin, als das hier nicht eine wiederholte Geburt in längeren Zwischenzeiten anzunehmen wäre."

SARS conjectures that the solitary fœtuses arise by a process of sexual generation, but does not state very clearly what he considers to be the nature of the production of the associated forms.

77. *The Placenta.*—CUVIER speaks of finding a fœtus attached to the parent by a pedicle; and referring to a figure, he says, "Ce corps rond (evidently the placenta) seroit-il un organe servant uniquement pendant le temps de la gestation pour établir l'union entre la mère et son petit et qui s'effaceroit ensuite?"

CHAMISSO calls the pedicle of attachment "pediculus umbilicalis;" the placenta, "globulus opacus."

MEYEN was the first to give this structure the name of placenta, and his account of it is so very clear and precise, that it is wonderful it should have been subsequently forgotten or overlooked. He says, "Wir haben bei ganz jungen Individuen den Verlauf der Blut-bewegung selbst bei 200-maliger Vergrösserung beobachten können. Der Muttertheil der Placenta hat nur wenige Gefässen um so mehr aber der Fötus-theil, in dem sich ein ausserordentliches Convolut von Gefässen befindet, das sich in einem Stämme endigt, der sich in das grosse Bauchgefäss ganz in der Nähe des Hergens ergiesst. Ein unmittelbares uebergehen der Blutgefässe ausdem Muttertheil in dem Fötus-theil haben wir nicht sehen können. Hat der Fötus die hinlängliche Ausbildung im Leibe der Mutter erreicht, so verwächst das grosse Blut-gefäss und die Placenta fällt ab."—P. 400.

78. After what has been stated concerning the development of the two forms of the *Salpæ*, it would be useless to enter upon the consideration of the various theories propounded since the time of CHAMISSO (such as that of ESCHRICHT for instance) to account for the phenomena they present.

It may be sufficient to say, that it is now quite certain that the *Salpæ* never unite after being once separated, and that they do not produce successive broods of a different form.

Much remains to be done with regard to the minute process of development of the young forms of both kinds, and to this difficult inquiry it is to be hoped that future observers will address themselves*.

In order to avoid the necessity of incessant references to the text, a list of the works consulted and alluded to, is here subjoined in chronological order.

Salpa.—FORSKAHL. Descriptiones Animalium, 1775.

BROWNE. Natural History of Jamaica, 1785.

* An essential service to zoology will be rendered by any one who will revise and critically compare the species of the *Salpæ*. At present, they are in a most unedifying state of hopeless confusion.

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